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Taxonomy of the Cyclostome Bryozoan *Liripora* MacGillivray and Some Related Australasian Taxa

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Taxonomic problems concerning the identity of the cyclostome bryozoan genus *Liripora* MacGillivray, 1887 are addressed. The valid type species of *Liripora* is *Diastopora fasciculata* MacGillivray, 1885, not *D. lineata* MacGillivray, 1885 as has often been assumed. This latter species is the type species of *Desmeplagioecia* Canu and Bassler, 1920 erroneously regarded as an objective junior synonym of *Liripora*. Scanning electron microscopic study of *Liripora* shows the genus to have an unusual colony construction: autozooids at distal growing edges have interior-walled peristomes that protrude above the level of a laterally extensive kenozooidal space bounded proximally by a sloping interior wall. Skeletally mature autozooids generally lack or have only very limited areas of exterior frontal wall s.s., the upper surface of the colony being formed instead by the calcified exterior frontal walls of the surrounding kenozooids. In addition to the type species, two new species from New Zealand—*Liripora pseudosarniensis* and *L. lobifera*—are placed in the genus, which appears to be endemic to Australasia. The three nominal species of *Liripora* are described, together with *Desmeplagioecia lineata* and a new species—*Mesenteripora triregorum*—that shows some resemblance to *Liripora*.

Key Words: Bryozoa, Cyclostomata, taxonomy, new taxa, morphology, New Zealand, Australia.

Introduction

The taxonomy of cyclostome bryozoans is poorly understood at all hierarchical levels. While contemporary bryozoological research has tended to focus on the more diverse and character-rich cheilostomes, cyclostomes have been relatively neglected. Species identification and generic attribution are greatly hindered in cyclostomes by a paucity of useful morphological characters (Taylor 2000). Nevertheless, recent work utilizing soft part anatomy (Boardman *et al.* 1992; Boardman 1998), the ultrastructural fabrics of skeletal walls (Taylor and Weedon 2000), and routine scanning electron microscopy of skeletal morphology (e.g., Harmelin 1976; Ostrovsky and Taylor 1996) has gone some way towards the achievement of a more refined taxonomy. Fundamental to this goal is a revision of generic definitions. The aim of the current paper is to revise one particularly problematical genus—

Liripora MacGillivray, 1887—which has been misinterpreted in some recent taxonomic works. *Liripora* is shown to have an unusual skeletal organization, not previously recognized in cyclostomes, which justifies its retention as a valid and probably monophyletic genus. Although colonies at first sight can be indistinguishable from other tubuliporine cyclostomes, such as *Plagioecia* and *Tubulipora*, they differ in having autozooids surrounded by kenozooids whose exterior frontal walls form most of the upper colony surface, unlike most other tubuliporines where this surface is formed by the exterior frontal walls of the autozooids.

The type species of *Liripora*—*L. fasciculata* (MacGillivray, 1885) from Australia—is redescribed, and two new species of *Liripora* from New Zealand are introduced. *Desmeplagioecia lineata* (MacGillivray, 1885), included in the original description of *Liripora* and later made the type species of *Desmeplagioecia*, is also redescribed, and an erect species from northern New Zealand that has some features in common with *Liripora* is described as *Mesenteripora triregorum* sp. nov.

All described specimens are in the collections of the National Institute of Water and Atmospheric Research, Wellington (NIWA), or The Natural History Museum, London (NHM).

Systematics

Order **Cyclostomata** Busk, 1852

Suborder **Tubuliporina** Milne-Edwards, 1838

Family **Diastoporidae** Busk, 1859

Genus ***Liripora*** MacGillivray, 1887a

Type species. *Diastopora fasciculata* MacGillivray, 1885; designated by Bassler (1935).

Revised diagnosis. Colony encrusting, multiserial, unilamellar; autozooids inclined at low angle to colony surface, opening at common bud of growing edge, in small fascicles continuous with common bud or on frontal surface proximally of common bud, either singly or in radial series; calcified exterior frontal walls present in autozooids in primary zone of astogenetic change, absent or slightly-developed in zone of astogenetic repetition; autozooids opening at distal growing edges with long, interior-walled ‘peristomes’, these apparently becoming exterior in older zooids and of variable length, bicuspsate terminations present in all stages; pseudoporous terminal diaphragms closing apertures of ontogenetically old autozooids; autozooids at growing edge surrounded by laterally extensive, shallow kenozooidal space backed by sloping, proximal interior wall; more proximal kenozooids with calcified frontal exterior walls overlapping interior-walled autozooidal peristomes and forming much of transversely rugose upper surface of colony, transverse furrows marking boundaries between successive bands of kenozooids; pseudopores large, closely-spaced, partly occluded by minute radial spines; nanozooids developed as secondary structures in some older or damaged autozooids, occasional questionable primary nanozooids also present; gonozooids equidimensional or transversely elongate, penetrated by some autozooidal apertures; ooeciostome terminal, short, distally-flared or straight; ooeciopore same size or somewhat smaller than adjacent autozooidal apertures; basal lamina skeletal ultrastructure foliated, comprising predominantly distally-imbricated crystallites.

Remarks. MacGillivray (1887a) proposed *Liripora* for two species he had previously described (MacGillivray 1885) from Port Phillip Heads, Victoria, as *Diastopora lineata* and *Diastopora fasciculata*. He regarded *Liripora* as distinct from true *Diastopora* 'in having the zooecia arranged in uni- or multiserial rows or ridges, and opening either along the summits of these ridges or towards their extremities' (MacGillivray 1887a: 182). Unfortunately, MacGillivray did not choose a type species for *Liripora* either in his original description of the genus or in a subsequent redescription (MacGillivray 1895: 138), in which a further two species were added to the genus, *Diastopora bicolor* MacGillivray, 1884 and *Liripora superposita* MacGillivray, 1895.

According to Bassler (1953: G54) the type species of *Liripora* is *D. fasciculata*. As pointed out by Walter (1987), the designation of this species as the type is attributable to Bassler (1935), who unequivocally indicated *D. fasciculata* as the 'genotype' of *Liripora*. However, Hayward and Cook (1983: 132) stated 'As the first species described in 1885 and the first listed in 1887, *L. lineata* may be regarded as the type species of *Liripora*,'. This is an invalid subsequent designation of the type species. Canu and Bassler (1920) later chose *Diastopora lineata* as the type species of their new genus *Desmeplagioecia*. Hayward and Cook (1983) concluded incorrectly that *Desmeplagioecia* was an objective junior synonym of *Liripora* because the two genera shared the same type species, an opinion repeated by Hayward and Ryland (1985: 104). *Desmeplagioecia lineata* is redescribed below and shown to be distinct from *Liripora*.

Discussion. Based on restudy of the type species and putative related species, the concept of *Liripora* is here revised to encompass forms with: (1) autozooids at the growing edge with interior-walled 'peristomes' that protrude above a surrounding kenozooidal space backed by a sloping interior wall (Figs 4, 5, 8, 14, 23); and (2) an upper colony surface formed largely from the exterior frontal walls of these kenozooids, apparently grown episodically, overlapping and partly covering the exposed interior-walled peristomes of the autozooids (Figs 3, 13, 17, 24). This unusual skeletal organization contrasts with other tubuliporine cyclostomes possessing similar discoidal encrusting colonies. In most tubuliporines the upper (frontal) surface of the colony is built from the frontal exterior walls of the autozooids. To illustrate this difference, a particularly instructive comparison can be made between *Liripora pseudosarniensis* sp. nov. from New Zealand waters and *Plagioecia sarniensis* (Norman, 1864 q.v.) from the north-east Atlantic and Mediterranean (see Harmelin 1976; Hayward and Ryland 1985). These two species have extremely similar colony-forms, and their almost identical auto-, nano-, and gonozooidal morphologies, plus similar pseudopore spinosity, led to initial misidentification of the New Zealand species as *P. sarniensis*. The budding zone of true *P. sarniensis* comprises a series of polygonal autozooidal buds (Hayward and Ryland 1985, fig. 34A), and the upper surface of the colony is constructed entirely of the exterior frontal walls of autozooids, plus gonozooids. In contrast, the budding zone of *L. pseudosarniensis* comprises autozooids with interior-walled 'peristomes' projecting into a kenozooidal space (Figs 8, 13, 14), and the upper surface of the colony is made mostly from the exterior frontal walls of kenozooids (Figs 9, 14, 17). A distinctive feature of *Liripora* is the 'use' of kenozooidal rather than autozooidal frontal exterior walls to form the upper colony surface and occupy the areas between the autozooidal apertures, thereby determining the spacing of the lophophores in liv-

ing colonies.

The budding zone or common bud of *Liripora*, with its functional autozooids having interior-walled autozooidal 'peristomes' surrounded by kenozooids, is reminiscent of certain free-walled cyclostomes, especially lichenoporidae. The mixture of free-walled and fixed-walled traits in *Liripora* parallels that found in another New Zealand family, the Cinctiporidae (Boardman *et al.* 1992), and further underscores the problems associated with conventional higher-level cyclostome classification, which separates free- and fixed-walled taxa at the subordinal level (Taylor 2000).

European species which have been assigned to *Liripora* either do not belong here or require restudy. These include species described by McKinney and Taylor (1997) from the British Cretaceous as *Liripora complanata* (Roemer, 1840), by Schattleitner (1991) from the Austrian Miocene as *Liripora biseriata* (Canu and Bassler, 1925) and *L. tenuis* (Reuss, 1869), and by Hayward and Ryland (1985) from the Recent of Britain as *Liripora amphorae* (Harmelin, 1976).

The three species of *Liripora* recognized here differ principally in the distributions and arrangements of the autozooidal apertures and, to some extent, in colony form. In *L. fasciculata* most of the autozooids open around the margin of the colony in radial, ridge-like fascicles, whereas autozooidal apertures are not aggregated into marginal fascicles and the colony surface lacks ridges in the two New Zealand species. The strongly lobate colonies of *L. lobulifera* enable this species to be distinguished from both *L. fasciculata* and *L. pseudosarniensis*, while the relatively even spacing of the autozooidal apertures on the colony surface is a unique attribute of *L. pseudosarniensis* among the three species.

Key to the Species of *Liripora*

1. Autozooids opening predominantly at growing edge; only a few isolated apertures on upper colony surface proximal to growing edge..... *L. fasciculata*
- Numerous autozooid apertures present on upper colony surface proximal to growing edge 2
2. Colony lobate; autozooidal apertures arranged in rows diverging from axes of lobes..... *L. lobulifera*
- Colony subcircular; autozooids generally arranged in quincunx..... *L. pseudosarniensis*

Liripora fasciculata (MacGillivray, 1885)

(Figs 1–6)

Diastopora fasciculata MacGillivray, 1885: 97, pl. 3, fig. 2.

Liripora fasciculata: MacGillivray 1887a: 182, 1887b: 218, 1895: 138, pl. 22, figs 4, 7; Jelly 1889: 139; Bassler 1935: 140, 1953: G54, fig. 22.2; Bock 2000, [3 figures].

Material. NHM 1897.5.1.1137, J. Bracebridge Wilson Collection, Port Phillip Heads, Victoria, Australia (topotype).

Revised diagnosis. *Liripora* with autozooids mostly grouped in fascicles and

opening around colony edge; colony subcircular, exposed basal lamina pustulose; fascicles forming ridges increasing in height distally; autozooids inclined at low angle to colony surface, interior-walled 'peristomes' bicusate at growing edge, apertures usually becoming biserially arranged within fascicles, short mural spines present; kenozooids opening as a continuous space between autozooids at growing edge, becoming sealed by distally concave exterior wall forming upper colony surface; pseudopores with radial spines; gonozooid transversely elongate, interrupting fascicles; oeciostome short, oeciopore about same size as autozooidal apertures, subcircular.

Description. Colony multiserial, unilamellar, encrusting, subcircular in outline, tending to be convoluted or twisted (Fig. 1), probably corresponding to shape of substratum (as noted by MacGillivray 1885), up to at least 7 mm in diameter. Edge of colony formed by broad basal lamina, pustulose and crossed by incipient vertical interior walls (septa) (Fig. 2). Frontal colony surface bearing few or no autozooidal apertures, rugose, with longitudinal ridges formed by autozooidal fascicles, and transverse folds and wrinkles, these latter distally concave between ridges and distally convex over ridges (Fig. 3). Pseudopores distributed unevenly over kenozooidal exterior walls, circular or subcircular in shape, large, about 10 μm in diameter, with tiny centripetal spines. Common bud with autozooids surrounded by broad kenozooidal space delimited proximally by sloping transverse wall (Fig. 4). Fascicles formed by clusters of low-angled autozooids, usually remaining connected with distal growing edge; upper (frontal) side inclined at low angle to basal lamina, distal face with apertures in plane almost perpendicular to basal lamina.

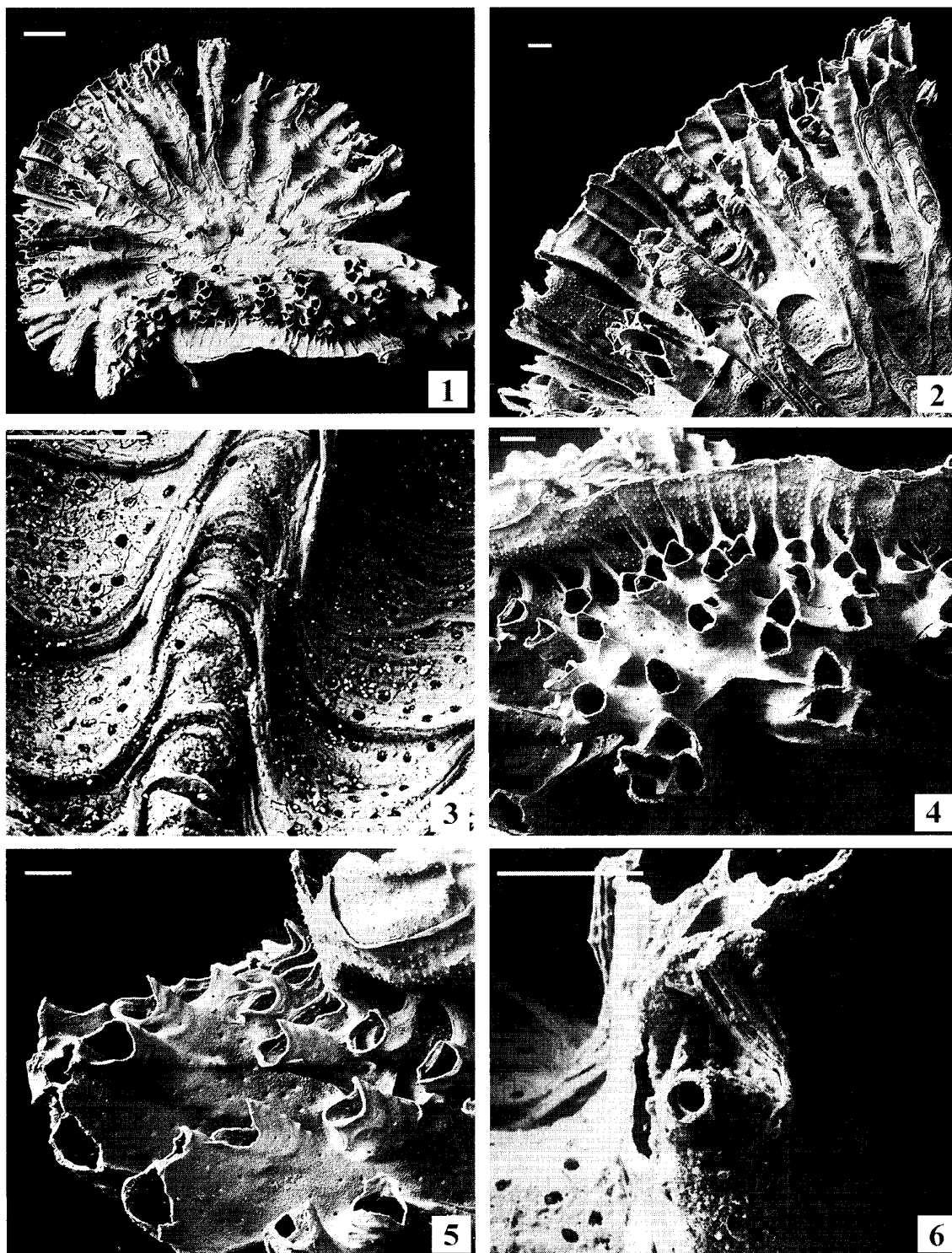
Autozooids mostly opening at common bud or in fascicles, initially isolated from one another but becoming arranged in uniserial series with growth upwards from basal lamina, and finally assuming an alternating biserial arrangement within fascicles. Young autozooids with isolated apertures and interior-walled 'peristomes', bicusate, with upper, proximal prolongation a little longer and more pointed than lower, distal one (Fig. 5). Apertural diameter small, 0.07–0.09 mm. Short mural spines visible in autozooids at growing edge. Apertures at growing edge sometimes occluded by interior wall continuous with proximal wall of kenozooidal space. Calcified exterior frontal walls of autozooids not developed or extremely limited and sparsely pseudoporous.

Kenozooids located between autozooids, forming extensive multizooidal space with sloping proximal porous walls at common bud, becoming roofed over by frontal exterior walls proximal to growing edge.

Primary nanozooids not observed. Secondary nanozooids sporadically developed, apertures about 0.02 mm in diameter, borne on short peristome arising from terminal diaphragm closing an autozooid (Fig. 6).

Gonozooid transversely elongate, interrupting autozooidal fascicles; oeciostome short, slightly flared, hidden between fascicles; oeciopore circular or longitudinally elongate, about same diameter as autozooidal apertures.

Remarks. The type locality of *L. fasciculata* is Port Phillip Heads, Victoria. MacGillivray (1895) also recorded fossil specimens from Muddy Creek and Moorabool, Victoria, both of Miocene age. According to P. L. Cook (*in litt.*, October 1999), the unique MacGillivray specimen of *L. fasciculata* in the Museum of Victoria (MOV H45439/65180), presumed to be the type, is affected by 'shell disease', shows



Figs 1–6. *Liripora fasciculata* MacGillivray, 1887, Port Phillip Heads, Melbourne, Australia, NHM 97.5.1.1137: 1, entire colony; 2, distal growing edge; 3, detail of upper colony surface showing sparsely pseudoporous autozooidal frontal wall *s.l.* (peristome) with distally concave, densely pseudoporous, kenozooidal frontal wall *s.s.* on either side; 4, growing edge in almost proximal aspect showing autozooidal interior-walled peristomes protruding from porous, sloping interior wall partitioning kenozooidal space; 5, lateral view of growing edge showing interior-walled peristomes of autozooids with bicuspsate terminations; 6, damaged secondary nanozooid. Scale bars: (1) 500 μm ; (2)–(6) 100 μm .

little detail, and is infertile.

In its original binomen—*Diastopora fasciculata* MacGillivray, 1885—this species is a junior homonym of *Diastopora fasciculata* Reuss, 1846 (*q.v.*) from the Cretaceous of Bohemia (E. Voigt, *in litt.*, October 1999). These two nominal species have been assigned to different genera since well before 1899; therefore, in accordance with Article 23.9.5 of the Code (International Commission on Zoological Nomenclature 1999), pending submission of a case to the Commission, the prevailing usage of both names is maintained.

The only specimen available for study is infertile. However, excellent scanning electron micrographs of a fertile colony were available on a web-page (Bock 2000), and these form the basis for the description of the gonozooid given above.

The well-developed fasciculate form of *L. fasciculata* sets it apart from other species of the genus. Harmelin (1975) regarded the progressive evolution of fasciculate colonies from non-fasciculate progenitors as a common trend in tubuliporine cyclostomes. *Liripora* perhaps furnishes another example of this trend: it is possible to devise a morphoserries running from *Liripora pseudosarniensis*, which has equidistantly-spaced, non-connate apertures, through *L. lobifera*, with variably connate apertures arranged in longitudinal series, to *L. fasciculata*, in which all or nearly of the apertures are aggregated in fascicles. However, without a broader analysis of cyclostome phylogeny, it is impossible to establish whether this morphoserries really does represent a unidirectional evolutionary pathway within the genus *Liripora*.

Distribution. Port Phillip, Melbourne, Victoria, and Deal Island, Bass Strait, Australia (Bock 2000).

***Liripora pseudosarniensis* sp. nov.**

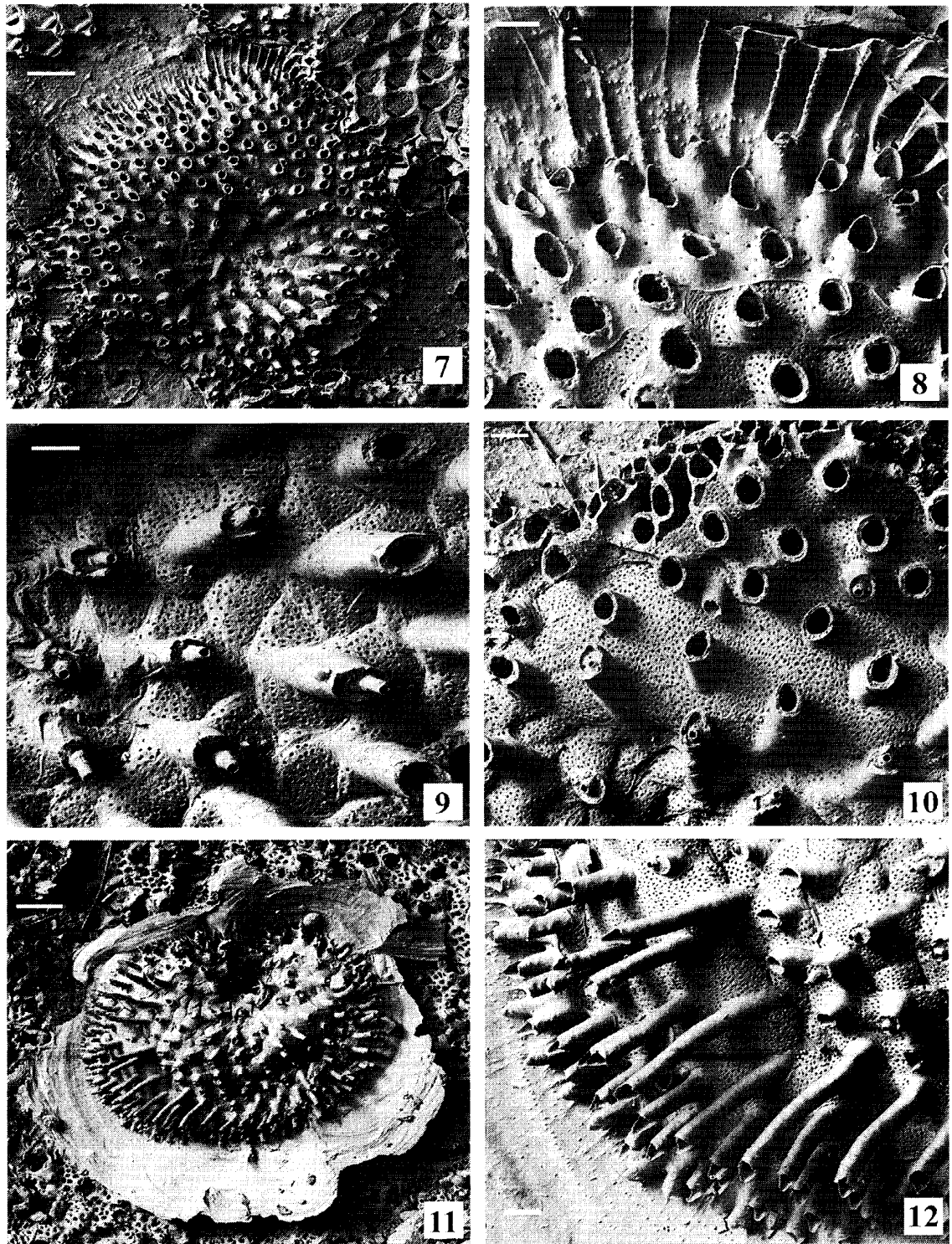
(Figs 7–18)

? *Diastopora sarniensis* Norman, 1864 var. *perangusta* Waters, 1887c: 342.

Material. Holotype: NIWA H-730, NZOI Stn Z9684, Spirits Bay, northernmost North Island, New Zealand, 40 m, 34°23.55'S, 172°51.72'E, 26 January 1999. Paratypes: NIWA P-1195, Echinoderm Reef, Goat Island Bay, Leigh, north of Auckland, New Zealand, intertidal, D. P. Gordon Collection; P-1196, NZOI Stn B235, four colonies on a pebble, Foveaux Strait, New Zealand, 49 m, 46°58'S, 167°92'E, May 1960; P-1197, NZOI Stn B246, eight colonies on a pebble together with other cyclostome and cheilostome species, 49 m, Foveaux Strait, New Zealand, 46°50'S, 167°92'E, May 1960; P-1198, NZOI Stn Z8850, one colony on a shell fragment, Spirits Bay, New Zealand, 36 m, 34°47.01'S, 173°13.01'E, 2 March 1997. Paratype: NHM 2000.7.12.1, same locality as holotype.

Etymology. In reference to the similarity with *Plagioecia sarniensis* (Norman).

Diagnosis. *Liripora* with autozooids opening on upper colony surface, not arranged in fascicles or radiating rows; colony fan-shaped or subcircular; autozooids from zone of astogenetic repetition with bicusgate interior-walled 'peristomes' at growing edge, lacking pseudoporous frontal walls but having low-angled, non-pseudoporous peristomes (? exterior walls) and longitudinally elongate aper-



Figs 7–12. *Liripora pseudosarniensis* sp. nov., NZOI Stn Z9684. 7–10, NIWA holotype H-730: 7, entire colony; 8, distal growing edge showing sloping interior wall supporting autozooidal peristomes; 9, proximal colony surface with secondary nanozooids and autozooidal peristomes surrounded by patches of kenozooidal frontal wall s.s. calcification; 10, gonozooid. 11–12, NHM 2000.7.12.1, paratype: 11, colony with raised edge formed by broad distal fringe of basal lamina; 12, long autozooidal peristomes with bicusperate terminations. Scale bars: (7), (11) 500 μm ; (8), (9), (10), (12) 100 μm .

tures, short mural spines present; autozooids from primary zone of astogenetic change with pseudoporous frontal walls; kenozooids opening as continuous space at distal growing edge, partitioned transversely by inclined interior walls and becoming roofed by exterior walls to form rugose upper colony surface between autozooids; pseudopores with radial spines; secondary nanozooids commonly developed, vicarious; gonozooid crescent-shaped, transversely elongate.

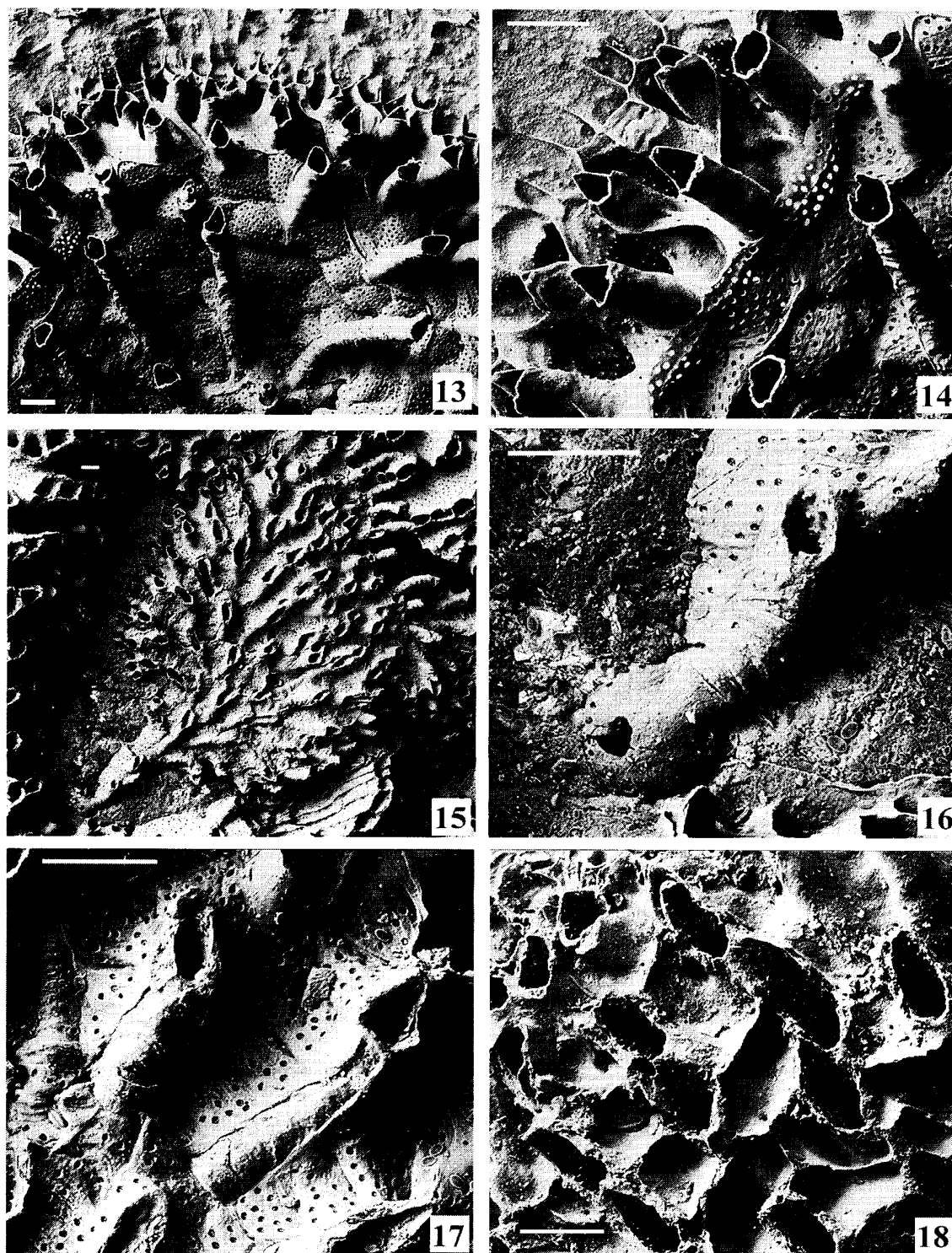
Description. Colony multiserial, unilamellar, encrusting, initially fan-shaped (Fig. 15) but becoming subcircular (Figs 7, 11) in outline, up to 4 mm in diameter and 0.4 mm in thickness. Distalmost circumference of colony formed by broad basal lamina up to 1.1 mm wide, occasionally lifting free of substratum (Fig. 11), usually non-pustulose but occasionally with distantly-spaced pustules, with incipient vertical interior walls (septa) developing back from margin. Frontal colony surface bearing numerous autozooidal apertures not arranged in radial series, rugose, with longitudinal folds formed by convex peristomes of autozooids, and transverse folds formed by patch-like (Figs 9, 13), convex exterior frontal walls of successive generations of kenozooids separated by grooves or steps, these latter sometimes exposing upper parts of transverse interior vertical walls between kenozooids. Pseudopores closely spaced and distributed relatively unevenly over kenozooidal frontal walls, circular or subcircular in shape, large, nearly $10\text{ }\mu\text{m}$ in diameter, mostly filled by minute centripetal spines. Common bud with autozooids surrounded by broad, variably subdivided kenozooidal space except when newly-formed (Fig. 14). Ancestrula (Fig. 16) with sparsely pseudoporous, narrow ($0.18 \times 0.06\text{ mm}$) frontal exterior wall; protoecium about 0.11 mm in diameter, with single row of pseudopores closely parallel to outer margin.

Autozooids opening at common bud and on frontal surface of colony, arranged more-or-less quincuncially on frontal surface (Figs 7, 8). Young autozooids in common bud with interior-walled 'peristomes', $100\text{ }\mu\text{m}$ or more in length and frequently curved, with bicusate terminations; lower, distal prolongation slightly longer than upper, proximal one (Fig. 14). Apertures of older autozooids opening on frontal surface of colony small and longitudinally elongate, about 0.08–0.12 by 0.05–0.08 mm in diameter. Peristomes usually short but reaching 0.6 mm in length and sometimes slightly curved (Fig. 12). Short mural spines visible within some autozooidal apertures (Fig. 18). Autozooids in zone of astogenetic repetition lacking frontal walls or having very limited and sparsely pseudoporous frontal walls s.s.; autozooids in zone of primary astogenetic repetition developing pseudoporous frontal walls (Fig. 15).

Kenozooids located between autozooids, forming broad multizooidal space at common bud, becoming subdivided by sloping, transverse interior walls with pores (Figs 8, 14), and eventually being roofed over by exterior frontal walls (Figs 9, 13, 17, 18). Kenozooids apparently lacking in zones of primary astogenetic change.

Secondary nanozooids (Fig. 9) developing within older autozooids, with terminal diaphragm supporting short peristome with tiny aperture about $10\text{--}15\text{ }\mu\text{m}$ in diameter.

Gonozooid (Fig. 10) transversely elongate (about 0.80 by 2 mm), crescent-shaped, paralleling distal margin of colony, with densely pseudoporous frontal exterior wall pierced by numerous autozooidal apertures. Ooeciostome short, almost straight, distally-flared, often bent over gonozooidal frontal wall. Ooeciopore subcircular, slightly smaller than autozooidal apertures, about 0.08–0.09 mm in diame-



Figs 13–18. *Liripora pseudosarniensis* sp. nov. 13–14, NZOI Stn Z8850, NIWA paratype P-1198: 13, part of colony showing distal growing edge and upper colony surface formed of patchwork of kenozooidal frontal walls s.s.; 14, detail of growing edge with advancing front of pseudo-porous frontal walls. 15–17, NZOI Stn B235, NIWA paratype P-1196: 15, small colony preserving early astogeny; 16, ancestrula; 17, distal colony surface with kenozooidal frontal walls lapping onto sides of autozooidal peristomes. 18, NZOI Stn B246, NIWA paratype P-1197, abraded colony surface showing autozooidal tubes (elongated parallel to growth direction, bottom right to top left) with mural spines and surrounded by kenozooids. Scale bars 100 μ m.

ter.

Remarks. *Liripora pseudosarniensis* can be distinguished from other species of *Liripora* by the evenly-spaced autozooidal apertures on the frontal colony surface. The remarkable similarity between this species and *Plagioecia sarniensis* has already been mentioned above. The external feature most useful in distinguishing *L. pseudosarniensis* from *P. sarniensis* and other sheet-like tubuliporines is the manner in which the autozooidal 'peristomes' protrude outwards from the growing edge (Fig. 14).

Waters' (1887c) 'variety' *perangusta* of *Plagioecia sarniensis* was described, although unfortunately not figured, on the basis of two specimens, one a fossil from Waipukurau (probably Pliocene), and the other a Recent specimen from an unspecified locality in New Zealand. Although it must now be regarded as an available species-group name (Code, Article 45.6.4), and thus may eventually turn out to be a senior synonym of *L. pseudosarniensis*, it is very difficult to assess the true identity of Waters' (1887c) variety. His description notes (pp. 342–343) that 'the younger zooecia run by the side of the older ones for some distance, thus causing the zooecia to be less crowded than is usually the case'. This may point to the existence of kenozooids between the autozooids like those seen in *L. pseudosarniensis*.

Distribution. Foveaux Strait, Leigh, and Spirits Bay regions of New Zealand.

***Liripora lobifera* sp. nov.**

(Figs 19–24)

Material. Holotype: NIWA H-731, NZOI Stn A444, on pebble, 192 m, Cook Strait, New Zealand, 41°24'S, 174°49'E, October 1958. Paratype: NIWA P-1199, details as for holotype.

Etymology. In reference to the lobate form of the colony.

Diagnosis. *Liripora* with lobate colonies having autozooids opening on colony surface in uniserial series distally divergent from axes of lobes; colony typically with regrowth from damaged older parts; kenozooidal space developed at shallow growing edge; pseudopores with radial spines; basal lamina non-pustulose; secondary nanozooids and rarer primary nanozooids present; gonozooid transversely ovoidal to subtriangular, slightly wider than long, penetrated by autozooidal peristomes.

Description. Colony multiserial, encrusting, strongly lobate (Figs 19, 20), compound and reaching up to 23 mm in diameter. Rejuvenative growth frequent in older parts, often including self-overgrowth of damaged remnants of earlier zooids. Distalmost edge of colony formed by non-pustulose basal lamina, variable in width, almost 1 mm wide in some embayments between lobes. Frontal colony surface covered by connate or non-connate autozooidal apertures arranged in curved uniserial rows diverging from lobe axes; rugose, with longitudinal folds formed by convex peristomes of autozooids, and with transverse bands of non-pseudoporous wall between slightly convex exterior frontal walls of successive generations of kenozooids. Pseudopores of kenozooids closely-spaced, large, circular or subcircular, partly occluded by centripetal spines. Growing edge shallow with autozooids surrounded by kenozooidal space delimited proximally by interior wall with pores (Fig. 23).

Autozooids opening at common bud, and on frontal surface of colony in curved uniserial rows parallel to local growth direction (Fig. 20). Young autozooids in common bud with short, interior-walled peristomes with bicusate terminations: lower, distal prolongation longer than upper, proximal one. Apertures of older autozooids opening on frontal surface of colony longitudinally elongate, about 0.09–0.15 mm long by 0.06–0.08 mm wide, usually without appreciable peristome. Frontal exterior walls of autozooids limited in area and with fewer pseudopores than adjacent kenozooidal frontal walls.

Kenozooids located between autozooids, forming broad multizoooidal space at common bud, becoming subdivided by transverse interior walls with pores, and eventually being roofed over by calcified exterior wall proximal to growing edge (Fig. 24).

(?)Primary nanozooids uncommon; apertures about 20 μ m in diameter with short peristome; secondary nanozooids common (Fig. 22), developing within older autozooids, slightly depressed terminal diaphragm of host autozoid supporting short peristome with small aperture.

Gonozooid (Fig. 21) transversely elliptical to subtriangular in outline, slightly wider than long (0.75–0.98 mm long by 0.98–1.23 mm wide), with densely pseudoporous roof pierced by six or more autozooidal peristomes, some hosting secondary nanozooids. Preserved oeciostomes broken, short, almost straight but somewhat distally flared. Oeciopore slightly smaller than autozooidal apertures, sub-circular, about 50–65 μ m in diameter.

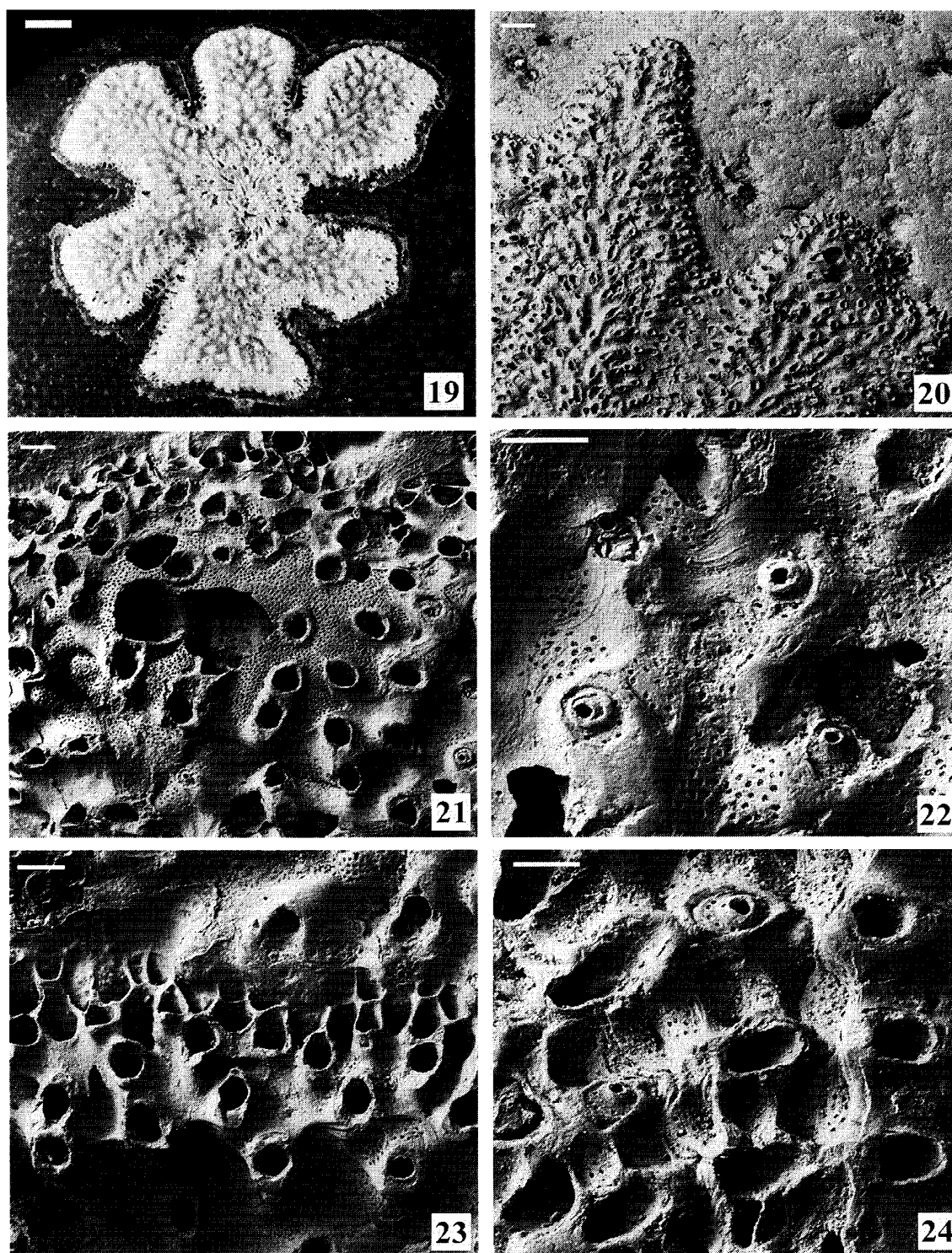
Remarks. The strongly lobate colonies (Fig. 19) allow this species to be readily distinguished from other species of *Liripora*. The holotype colony covers about a third of the total surface of a pebble 35×23×10 mm in size and comprises two patches of zooids that were once apparently joined together. Different parts of this colony exhibit variable preservational states: distal areas close to the growing edge are white and pristine, but older, more proximal areas are discoloured, or in extreme cases reduced to the basal lamina and abraded stumps of the vertical interior walls. Damaged parts of the colony may be overgrown by younger zooids. The smaller paratype colony also appears to have resulted from regrowth, and, as in the holotype, the white and pristine distal zooids are clearly demarcated from the discoloured proximal zooids. These observations suggest that colonies of *L. lobifera* are relatively long-lived perennials, growing episodically (seasonally?) and sustaining damage while alive, perhaps due to abrasive rolling of the pebble substrates they encrust.

Distribution. Cook Strait, New Zealand.

Genus *Desmeplagioecia* Canu and Bassler, 1920

Type species. *Diastopora lineata* MacGillivray, 1885; by original designation. Note that Canu and Bassler (1920) misquoted MacGillivray's species as *Berenicea lineata* MacGillivray, probably following Harmer (1915), who had assigned the species to this genus which is a *nomen dubium*; see Taylor and Sequeiros (1982).

Revised diagnosis. Colony encrusting, multiserial, discoidal, sometimes compound; growing edge with broad, exposed fringe of basal lamina crossed by septa, bearing sparse pustules and having foliated ultrastructural fabric of elongate, dis-



Figs 19–24. *Liripora lobifera* sp. nov., NZOI Stn A444. 19, NIWA paratype P-1199, lobate colony on pebble. 20–24, NIWA holotype H-731: 20, edge of large colony; 21, gonozooid with broken frontal wall; 22, secondary nanozooids in damaged part of colony; 23, detail of growing edge showing sloping, transverse proximal wall; 24, nanozooids and irregular kenozooidal frontal wall calcification extending between transverse walls. Scale bars: (19) 1 mm; (20) 500 μ m; (21)–(24) 100 μ m.

tally-imbricated crystallites; autozooids fixed-walled; frontal walls with small, unornamented pseudopores; apertures isolated in early astogeny, subsequently grouped into low, longitudinal fascicles, initially uniserial but becoming biserial or triserial, new fascicles originating by intercalation; apertures mostly closed by centripetally-accreted terminal diaphragms; gonozooid transversely elongate, interrupting about four fascicles; ooeciostome terminal with transverse ooeciopore; nanozooids lacking.

Remarks. Canu and Bassler (1920) apparently based their concept of this genus on Harmer's (1915) redescription of the type species and they reproduced Harmer's pl. 11, fig. 7 as their fig. 234. This figure was later re-used by Bassler (1953, fig. 22.9). It is likely that Harmer's Indonesian material of *Berenicea lineata* is not conspecific with MacGillivray's (1885) Victorian material of *Diastopora lineata*, in which case there are grounds for regarding *Desmeplagioecia* to have been founded on a misidentified type species. Article 70.3 of the Code (International Commission on Zoological Nomenclature 1999) deals with such misidentified type species and we herein apply its provisions to fix *Diastopora lineata* MacGillivray, 1885 as the type species of *Desmeplagioecia*.

In addition to the type species, Canu and Bassler (1920) referred 11 further species to *Desmeplagioecia*, six of them new, ranging from Cretaceous to Recent in age. Subsequent bryozoologists generally avoided the genus. Notable exceptions are Harmelin (1976), who assigned two new Mediterranean species to *Desmeplagioecia* (*D. amphorae* Harmelin, 1976 and *D. violacea* Harmelin, 1976), and Moyano (1983), who referred a new South American species (*D. irregularis* Moyano, 1983) to the genus. It is unlikely that any of these three species really does belong to *Desmeplagioecia*. Although the Mediterranean species all have similar colony-forms to *Desmeplagioecia lineata*, with proximally connate zooidal apertures forming biserial or triserial radial fascicles, the autozooids of these two species have long peristomes that diverge and become free distally, a condition not seen in the short fascicles of *D. lineata*. Moyano's (1983) species may be more correctly assigned to *Desmediaperoecia* Canu and Bassler, 1920 in view of its strong resemblance to the type species of this genus (see also Voigt 1987).

A critical re-evaluation, beyond the scope of the current paper, is clearly needed of other tubuliporine cyclostome genera with autozooidal apertures arranged in radial fascicles or rows. These include *Theonoo* Lamouroux, *Actinopora* d'Orbigny, *Discotubigera* d'Orbigny, *Seguenziella* Neviani, *Desmatelesia* Canu and Lecomte, and *Poroplagioecia* Weitschat and Voigt. For example, Gregory (1909: 5) thought that *D. lineata* belonged in *Actinopora*, and the transversely elongate gonozooid of *D. lineata* (Waters 1889, pl. 15, fig. 5) certainly does resemble that found in species of the predominantly Cretaceous *Actinopora*. Provisionally, however, *Desmeplagioecia* is here retained and placed in the Diastoporidae, a family embracing a wide variety of multiserial tubuliporines.

***Desmeplagioecia lineata* (MacGillivray, 1885)**
(Figs 25–30)

Diastopora lineata MacGillivray, 1885: 96, pl. 3, fig. 1 (non *Diastopora lineata* Gabb and Horn, 1862: 172, fig. 62).

Discotubigera (?) *lineata*: Waters 1887a, pl. 6, fig. 24, 1887b: 260, 1889: 284, pl. 15, fig. 5.

Liripora lineata: MacGillivray 1887a: 182, 1887b: 219; Jelly 1889: 139; Hayward and Cook 1983: 132.

?non *Berenicea lineata*: Harmer 1915: 116, pl. 11, figs 6–7.

?non *Desmeplagioecia lineata*: Canu and Bassler 1920: 718, fig. 234; Bassler 1935: 91, 1953: G54, fig. 22.9; Brood 1976: 284; Walter 1987, fig. 4.

Material. NHM 1897.5.1.1138, 1139, J. Bracebridge Wilson Collection, Port Phillip Heads, Victoria, Australia; NHM 1897.5.1.1140, J. Bracebridge Wilson Collection, locality not given; NHM 1963.2.12.19, Dundee Collection, Port Western.

Description. Colony multiserial, unilamellar, encrusting, circular or more commonly elliptical in outline (Figs 25, 29), sometimes apparently compound, individual subcolonies attaining diameter of at least 11 mm. Dried colonies sometimes retaining strong purple pigmentation, especially at growing edges. Distalmost edge of colony formed by broad basal lamina, often more than 1 mm wide, crossed for most of its width by low septa (incipient vertical interior walls) and bearing widely-spaced pustules; pustules also seen in exposed vertical interior walls of autozooids and kenozooids (Fig. 26). Autozooidal apertures isolated in early astogeny (Fig. 27), but in later astogeny becoming clustered into radial fascicles of low profile, initially containing uniserial series of apertures, later biserial and triserial, with occasional new fascicles becoming intercalated between existing fascicles during growth. Autozooidal frontal walls slightly raised and bearing faint, distally convex growth checks. Pseudopores widely-spaced, circular, small ($<3\mu\text{m}$ in diameter), and lacking spines (Fig. 28). Common bud of growing edge wide, comprising polygonal zooidal tubes of relatively constant size (Fig. 26); no clear differentiation between autozooids and kenozooids except close to frontal surface of colony, here some autozooidal apertures developing slight spinose prolongations on their lower (distal) edges.

Autozooids opening at common bud and on frontal surface of colony. Apertures opening on frontal surface longitudinally elongate, less commonly circular, about 0.08–0.12 mm long by 0.08–0.11 mm wide, most being closed by pseudoporous terminal diaphragms (Figs 27, 28) located just beneath distal rim, usually depressed centrally and having radial surface fabric.

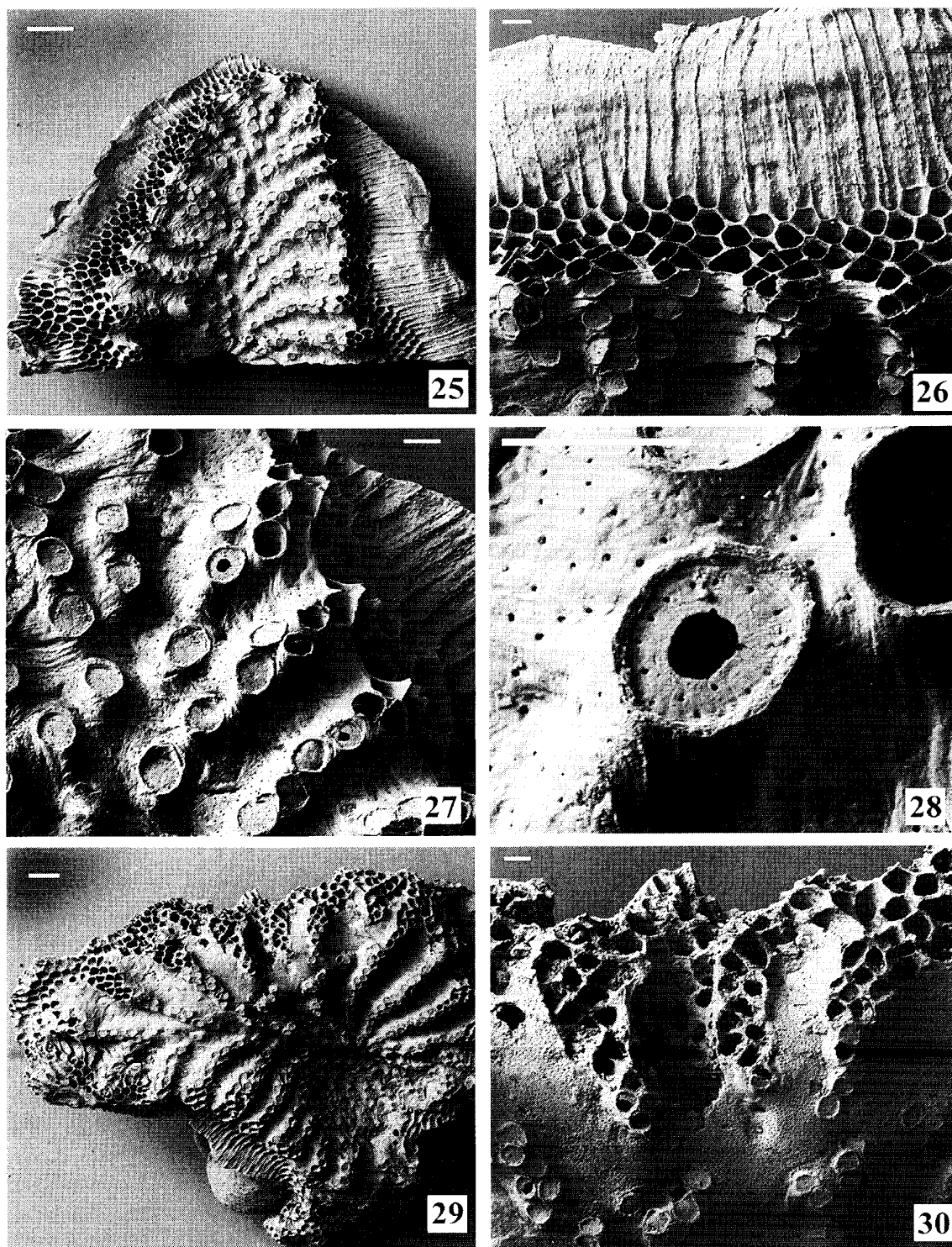
Kenozooids apparently developed between autozooidal series, probably present in smaller numbers than autozooids and seemingly wanting in earliest astogenetic stages.

Nanozooids not observed.

Gonozooid (Fig. 30) transversely elongate (1.6 mm long \times 2.9 mm wide in specimen 1963.2.12.19), interrupting and spanning about 4 fascicles, its roof densely pseudoporous and exhibiting sutures where patches of calcification from different loci meet. Ooeciostome terminal and ooeciopore transversely elongate.

Skeletal ultrastructure of exposed basal lamina foliated, with elongate, distally-imbricated crystallites having interfacial angles of 94–117°; imbrication becoming less regular at common bud.

Remarks. The MacGillivray Collection in the Museum of Victoria contains the figured type of this species (MOV H45440a/65170), together with several other slides (H45440/65172–9) (P. L. Cook, *in litt.*, October 1999). As with *L. fasciculata*, however, this material has suffered from ‘shell disease’ and shows little detail even



Figs 25–30. *Desmeplagioecia lineata* (MacGillivray, 1885). 25–28, Port Phillip Heads, Melbourne, Australia, NHM 1897.5.1.1139: 25, broken colony with broad distal fringe of basal lamina; 26, detail of growing edge showing budding zone and basal lamina with septa; 27, transition from early astogenetic zone with isolated autozooidal apertures (all closed by terminal diaphragms) to later zone with apertures aligned in fascicles; 28, developing terminal diaphragm showing centripetal pattern of calcification. 29–30, Port Western, Australia, NHM 1963.2.12.19: 29, fertile colony; 30, broken gonozooid. Scale bars: (25), (29) 500 μm ; (26), (27), (28), (30) 100 μm .

when cleaned.

In its original binomen—*Diastopora lineata* MacGillivray, 1885—this species is a junior homonym of *Diastopora lineata* Gabb and Horn, 1862 from the Paleocene of New Jersey, USA (E. Voigt, *in litt.*, October 1999). In accordance with Article 23.9.5 of the Code (International Commission on Zoological Nomenclature 1999) concerning homonymous species that have not been considered congeneric after 1899, pending submission of a case to the Commission to conserve the younger name, the prevailing usage of both names is maintained.

Distribution. Originally described from Victoria, Australia, this species was subsequently recorded from Indonesia, Singapore, and Japan by Harmer (1915) and from East Africa by Brood (1976). However, the non-Australian records are very doubtful.

Geuns *Mesenteripora* de Blainville, 1830

Mesenteripora triregorum sp. nov.

(Figs 31–40)

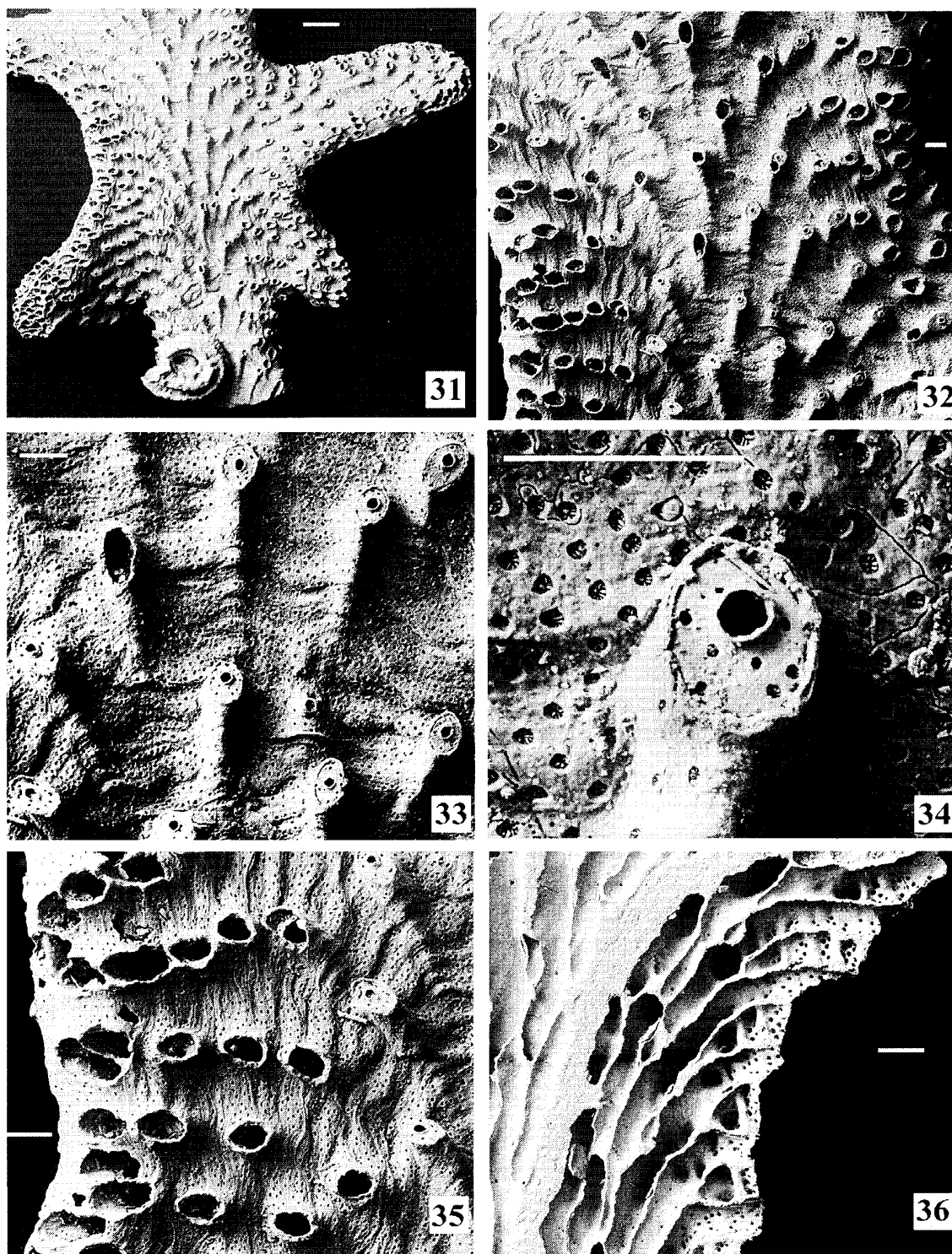
Material. Holotype: NIWA H-732, Three Kings Islands, New Zealand, 40 m. Paratypes: NIWA P-1200 (5 scanned plus 20 unscanned branch fragments), Three Kings Islands, 40 m; P-1201 (13 branch fragments), NZOI Stn Z9686, 48 m, 34°21.60'S, 172°41.14'E, 27 January 1999. Paratypes: NHM 2000.7.12.2–7 (6 unscanned branch fragments), Three Kings Islands, 40 m.

Etymology. Latin, from three (*tri*) and king (*regorum*; genitive form of *rex*) referring to the type locality, Three Kings Islands.

Diagnosis. *Mesenteripora* with narrow, twisted, strap-like branches; autozooids divergent from branch axis, those near axis with widely-spaced apertures, those close to branch margins with apertures in oblique lines, closely spaced, often connate; secondary nanozooids common; gonozooid frontal wall bulbous, penetrated by autozooidal apertures, generally asymmetrical in outline shape.

Description. Colony erect, multiserial, bilamellar, branches strap-like, narrow (*ca* 2–3 mm wide) and often twisted, bifurcating at irregular intervals, sometimes with short branches diverging from longer main branch in palmate pattern (Fig. 31), branch thickness about 0.45 mm; common bud of growing edge extending proximally for some distance down branch sides. Base of colony unilamellar, sometimes hollow (cavariiform), producing more than one erect branch. Surface of colony rugose with folds and furrows transverse to local growth direction (Figs 32, 33, 35).

Autozooids fixed-walled; frontal wall convex distally, flat proximally, with pseudopores about 6 μ m in diameter partly filled by tooth-like spines growing centripetally from circumference (Fig. 34); internally frontal wall in marginal zooids with transverse thickenings (Fig. 36); inclined at low angle to colony surface, diverging from branch axis with apertures quincuncially arranged and distantly spaced near branch axis (Fig. 33), becoming closely spaced, eventually connate, and aligned in curved rows near branch margins (Fig. 35); apertures small, longitudinally elongate, 0.09–0.15 mm long by 0.06–0.08 mm wide, most axial apertures filled by secondary nanozooids; peristomes normally short but occasionally reaching 0.5 mm in length.



Figs 31–36. *Mesenteripora triregorum* sp. nov., Three Kings Islands, New Zealand. 31–35, NIWA paratype P-1200a: 31, part of palmate colony fouled proximally by polychaete tube; 32, detail of branch showing distantly-spaced autozooidal apertures in axis giving way to apertures arranged in connate rows near margins of branch; 33, secondary nanozooids and one (?) primary nanozooid in axial part of branch; 34, secondary nanozooid and pseudopores partly filled by radial spines; 35, aligned autozooidal apertures at branch margin. 36, NIWA paratype P-1200b, ground branch showing thick, obliquely-sectioned median budding lamina (left) and undersides of frontal walls with periodic thickenings (right). Scale bars: (31) 500 μ m; (32)–(36) 100 μ m.

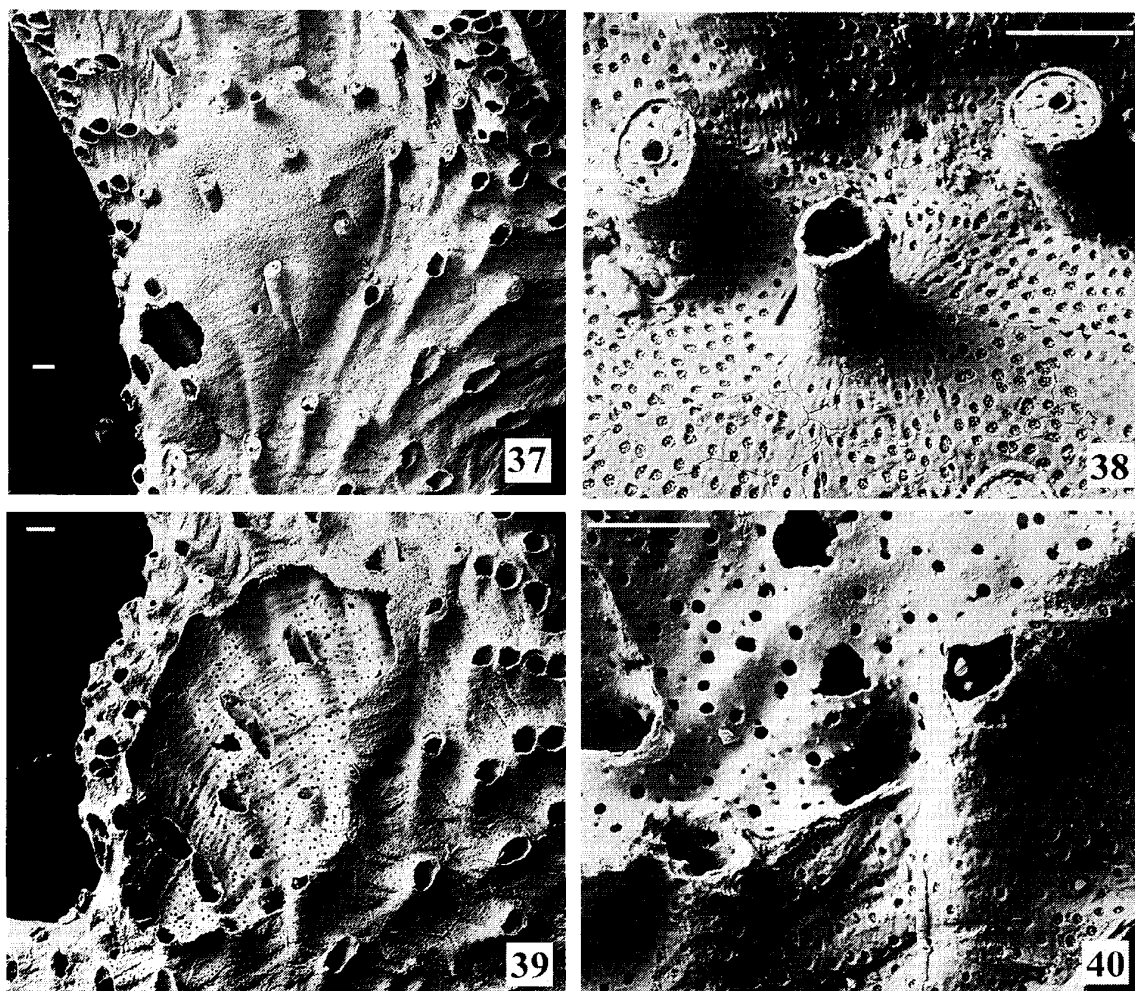
(?)Primary nanozooids (Fig. 33) rare, vicarious, with apertures about 0.02 mm in diameter. Secondary nanozooids common (Figs 33, 34), found in most axial autozooids, with short, tapering peristome originating from centre of terminal diaphragm, latter bearing sparse pseudopores about 3 μ m in diameter; aperture about 0.02 mm in diameter, circular or longitudinally elongate.

Gonozooids (Figs 37, 39) bulbous, normally asymmetrical but symmetrical when located immediately before branch bifurcation, extending further distally near branch axis than at margin, transversely elongate, 0.95–1.81 mm in length by 1.95–2.10 mm in width ($n=3$), proximal edge almost straight, distal edge strongly convex, penetrated by autozooidal apertures; floor with scattered, low pustules and holes of varying sizes (Figs 39, 40), larger ones interpreted as borings but smaller ones more likely to be interzooidal pores; ooeciostome almost terminal, tubular, straight sided, directed distally; ooeciopore (Fig. 38) slightly smaller than adjacent autozooidal apertures, about 0.05–0.06 mm in diameter.

Remarks. This new species is described here because it exhibits certain morphological similarities with *Liripora*, notably the presence of secondary nanozooids, the structure of the gonozooid, and the tooth-like spines growing into the pseudopores. The colony surface has a *Liripora*-like rugosity but, unlike *Liripora*, this is not due to episodic growth of kenozooidal exterior walls but apparently reflects periodic transverse thickening of the undersides of the autozooidal frontal walls (Fig. 36).

Bifoliate taxa are found throughout the Mesozoic-Recent fossil record of tubuliporine cyclostomes but seem to have diminished in importance from a maximum in the mid-Jurassic to a relatively small number at the present day. Extant species include *Bidiastopora torquata* Kirkpatrick, 1888 (*q.v.*), '*Cardioecia*' *watersi* (O'Donoghue and de Watteville, 1939 *q.v.*) (see Harmelin 1976), *Plagioecia dorsalis* (Waters, 1879 *q.v.*) (see Harmelin 1976), *Diplosolen intricarius* (Smitt, 1872) (see Kluge 1975), *Mesenteripora meandrina* (Wood, 1844 *q.v.*) (see Kluge 1975), *Diaperoecia meandrina* Canu and Bassler, 1930 (*q.v.*), and *Plagioecia reticuloides* Canu and Bassler, 1929 (*q.v.*). Of these species, *Plagioecia dorsalis*, *Diplosolen intricarius*, *Diaperoecia meandrina*, and *P. reticuloides* have *Reticulipora*-like colonies in which frond bifurcation occurs in a plane at right angles to the budding lamina and the fronds typically form a polygonal boxwork structure, a colony-form very unlike that of *Mesenteripora triregorum*. Colonies of *Mesenteripora meandrina* constitute corrugated, broad fronds filling an overall spheroidal envelope of space, and contrast with the narrow, strap-like branches found in the new species. *Bidiastopora torquata* and '*Cardioecia*' *watersi* both have narrow branches, but in neither case are the marginal autozooids aligned in rows, and both species have branches more nearly circular in cross-section. Furthermore, the autozooids in the type specimen (NHM 1888.5.17.11) of the Australian species *B. torquata* are appreciably larger than those of *M. triregorum*. A fossil bifoliate tubuliporine from New Zealand was described by Stoliczka (1865) as *Mesenteripora rerehauensis*. This Orakei Greensand (Lower Miocene) species lacks the distinctive divergent arrangement of autozooids seen in *M. triregorum*. In contrast with *M. triregorum*, neither of the two Australasian species (*Mesenteripora rerehauensis* and *Bidiastopora torquata*) is known to possess nanozooids, although the Arctic species *Diplosolen intricarius* does have them.

Distribution. Northernmost New Zealand (Three Kings and Spirits Bay re-



Figs 37–40. *Mesenteripora triregorum* sp. nov., Three Kings Islands, New Zealand. 37–38, NIWA holotype H-732: 37, gonozooid; 38, ooeciostome (centre) and two secondary nanozooids. 39–40, NIWA paratype P-1200e: 39, gonozooid without roof; 40, detail showing apparent entrance to fertile zooid (centre) and floor of gonozooid with tubercles and holes interpreted as pores (smaller, countersunk holes) and borings (larger holes). Scale bars 100 μ m.

gions). Putatively conspecific fossil material occurs in the Lower Miocene Forest Hill Limestone of Southland, New Zealand (NHM Palaeontology Collections), but this requires further investigation before its identity can be confirmed.

Discussion: Skeletal Organization of *Liripora*

Without the resolving power of SEM, species of *Liripora* are externally almost indistinguishable from several other tubuliporine genera including *Actinopora* and *Plagioecia*. The distinctive skeletal organization of *Liripora* becomes clearly evident only when colonies are scanned. The interpretation of body wall types presented here (below and Table 1) is based entirely on skeletal morphology and requires testing using anatomical studies beyond the scope of this paper. In particu-

Table 1. Comparison of skeletal wall development in a typical tubuliporine (*Plagioecia*) with that in the autozooids and kenozooids of *Liripora*.

frontal wall component	<i>Plagioecia</i> autozoid	<i>Liripora</i> autozoid	<i>Liripora</i> kenozooid
1. frontal walls s.s.	present; exterior-walled	absent	present; exterior-walled
2. peristomes	present; exterior-walled	present; initially interior-walled, becoming exterior-walled	absent
3. terminal diaphragms	present; exterior-walled	present; exterior-walled	absent

lar, confirmation of the distinction between interior and exterior walls, formed respectively as internal partitions of body cavity and at the bryozoan-environment interface, demands hard-soft sections showing relationships between soft tissues and the skeleton.

Cyclostome skeletal walls comprise a succession of topologically defined components which are normally formed sequentially during the ontogeny of each zooid, although not all of these components are necessarily present in every species (Taylor 2000). The first wall component is the basal wall, an interior or exterior wall (basal lamina) forming the floor of the zooid in encrusting and some erect species. This is followed by vertical, interzooidal walls, which are interior walls normally shared by adjacent zooids and present in all extant species of cyclostomes. In the context of *Liripora*, the succeeding frontal wall complex is particularly important. Frontal wall complexes consist of up to three components: (1) frontal walls in the restricted sense (s.s.) which are oriented more or less transversely to the local axis of zooidal growth and accrete in a proximal to distal direction; (2) peristomes oriented parallel to the local axis of growth and also accreting distally; and (3) terminal diaphragms oriented transversely to the growth direction, accreting centripetally and sealing the zooid. All three frontal wall components are most often exterior walls, although examples are known of interior wall versions of these topologically defined wall components.

Skeletally immature autozooids visible at distal growing edges in *Liripora* have bicusate, tubular prolongations around their apertures (Figs 5, 14). These are interior-walled structures that have a peristome-like morphology. They commonly extend distally from a sloping interior wall into a multizooidal space. This arrangement of bicusate autozooidal tubes surrounded by multizooidal space contrasts with other tubuliporines, in which the openings of autozooids at the growing edge are polygonal in shape and flush (*e.g.*, Fig. 26), and kenozooids, if present at all, take the form of simple polygonal tubes resembling those of the autozooids but generally of a smaller size. Skeletally mature zooids also differ between *Liripora* and other tubuliporines. In most tubuliporines the upper colony surface is formed of the calcified frontal exterior walls of autozooids, but in *Liripora* this surface consists of the calcified exterior frontal walls of kenozooids accreting distally and therefore regarded as frontal walls s.s. rather than terminal diaphragms. The auto-

zooids of *Liripora* in zones of astogenetic repetition lack the extensive pseudoporous, exterior frontal walls s.s. that characterise most other tubuliporines (and articulate cyclostomes), although such walls are present in the primary zone of astogenetic change of at least one species, *L. pseudosarniensis* (Fig. 15). The small areas of autozooidal wall (Figs 9, 17) that are usually visible on the colony surface between the kenozooidal frontal walls are best interpreted as low-angled peristomes rather than frontal walls s.s. in view of their continuity proximally with the interior-walled 'peristomes' found in the immature autozooids at the growing edge, and distally with peristomes growing free of the colony surface (Fig. 12). The latter have the texture of exterior walls even though pseudopores are rare to absent. Finally, exterior-walled terminal diaphragms may grow centripetally across the aperture in *Liripora*. These tend to be partial, containing small, central tubes which, by analogy with similar structures in *Plagioecia*, are interpreted as secondary nanozooids (Figs 9, 22).

The unusual skeletal organization in *Liripora* can be partly explained by the deletion of frontal walls s.s. from the ontogenetic sequence of the skeletal wall components of autozooids, i.e. interior vertical walls in *Liripora* autozooids are followed by interior peristomes without the intervening frontal wall s.s. stage. A second unusual feature is the presence of a laterally extensive cavity surrounding the autozooids at the colony growing edges (Figs 4, 5, 8, 13, 14, 23). This cavity becomes subdivided by obliquely-sloping interior walls ('vertical walls'), thereby partitioning off a series of kenozooids (Fig. 18). The calcified exterior frontal walls s.s. (Figs 9, 13, 14) of these kenozooids form the upper colony surface, a surface which is normally formed in tubuliporines by the frontal walls s.s. of autozooids. Whereas the spacing between apertures of mature autozooids in typical non-fasciculate tubuliporines is effectively determined by the dimensions of the frontal walls s.s. of these autozooids, in non-fasciculate species of *Liripora* this 'role' is fulfilled by the frontal walls s.s. of the kenozooids.

Acknowledgements

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